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THE WHITEFISHES

(Coregonus clupeaformis)

A STUDY OF THE SCALES OF WHITEFISHES OF KNOWN AGES[2]

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INTRODUCTION.

During recent years many investigations of scientific and economic importance have been conducted on the age and the rate of growth of fishes as determined from a study of their scales. This has involved the interpretation of certain rings found on the exterior surface of scales.

In order to illustrate clearly the mode of the formation of these rings, Fig. 137 is presented. It represents a typical scale of a whitefish, 197 mm. in length, captured October 22, 1917, at East Tawas, Mich., on Lake Huron. Near the center of the scale is a small, clear area, the focus (F), which represents the original scale in the young specimen. Around this focus are numerous, more or less relieved striations, concentric or nearly so with the margin. These are termed circuli (C) and like the rings in a tree mark successive stages in the growth of the scale. Running from the focus to the periphery of the scale are four more or less conspicuous radiating ridges (AR, PR), which divide the surface of the scale into four roughly triangular areas or fields. When the scale is in position in the fish the area to the right in the figure is directed towards the tail and is therefore designated as the caudal or posterior area (Caudal). The area opposite the caudal is the anterior (Anterior), while the two areas which separate the caudal from the anterior are the lateral or the dorsal (Dorsal) and the ventral (Ventral). The borders of these four areas which form the periphery of the scale are accordingly termed the caudal, anterior, dorsal and ventral

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borders. The radiating ridges are either antero-lateral (AR) or postero-lateral (PR). The greatest antero-posterior diameter which bisects the caudal area of the scale is its length (L-L).

By careful examination two distinct zones may be seen in this scale, an inner characterized in general by more closely spaced lines and an outer in which the lines are further apart. The two zones are more readily seen when the figure is viewed from such a distance as to somewhat obscure the details. The inner zone represents, according to current theory, the entire growth of the first year, while the outer zone represents the growth of the second summer. If the lines of growth in the lateral field be followed from the center outward and downward along the antero-lateral ridge, it may be seen that the first twenty are complete and uniformly spaced. With occasional breaks and irregularities they may be traced entirely around the scale. The next six are incomplete and the outermost of them ends (or begins) near the antero-lateral ridge. Following this last incomplete line to the anterior field, a region is encountered within which the individual circuli can no longer be traced with certainty, for they are less distinct, much broken, anastomosed and closer together. This zone of faint, approximated and much broken circuli, when contrasted with the preceding and succeeding areas of strong, complete and widely spaced circuli stands out as a rather sharply defined band. This band may be traced around the whole scale and is perhaps better defined in the posterior field where it appears as a lighter zone with very little detail.

To account for these structures, it is contended that the completed and comparatively widely separated circuli are formed during periods of rapid growth, the incomplete lines during periods of decreased growth, and the short, weak, much broken lines during periods when growth has nearly ceased. As the cessation or retardation of growth is thought to occur in the winter, the much broken area is accordingly designated as a winter-band or annulus (A).

When the scale resumes its growth in the spring a complete circulus is again formed which in the process of uniting, as it were, the incomplete lines bends sharply at the antero-lateral ridge. This circulus is considered the limit of the annulus it encloses and is so employed in the measurements of scales.

The twenty-five circuli of the second summer, in this scale, are much more widely separated than those of the first, which indicates a much more rapid growth during the former season.

Of these twenty-five circuli the last five or six at the margin are incomplete, which indicates the occurrence of a retardation in growth. No approximation of the circuli is yet visible, nor is there apparent the area of weak and broken lines. A complete cessation of growth has not yet taken place. This conclusion appears to be reasonable as the specimen was caught in October preceding the period of low temperatures when growth is greatly retarded or ceases altogether.

The foregoing account of the mode of formation of annuli is accepted by the majority of those investigators who make use of scales in determining the lengths and rate of growth of fishes.

The application of the above hypothesis to the study of the life-histories of fishes is a simple matter. By enumerating the annuli on the scales, the age of the individual is determined in years. Thus the specimen whose scale (Fig. 137) illustrated the method of growth is found to be at the end of its second year. The length of an individual at the end of each successive year may also be ascertained from its scales. Given the total length of the fish and of one of its scales and the length of that part of this scale included in an annulus formed during a given year, the total length of the fish at the end of this given year may be computed by the following formula in which the third term is the unknown:

$$\frac{\text{length of scale formed at end of year X}}{\text{total length of scale}} = \frac{\text{length of fish at end of year X}}{\text{length of fish at the time of capture.}}$$

Repeating this formula for each year of the fish's life, the lengths attained at the end of the several years are calculated and by a simple subtraction the increments of growth for each year are determined.

The soundness of the scale method of determining the length of a fish at successive years of its life and its annual growth increments depends on the validity of the following propositions:

1. That the scales remain constant in number and identity throughout the life of the fish.
2. That the annual increment in the length (or some other dimension which must then be used) of the scale maintains throughout the life of the fish a constant ratio with the annual increment in body length.
3. That the annuli are formed yearly and at the same time each year.

Incidentally the following questions are raised, but the validity of the scale method of computation is not affected by them:

4. Whether the annuli represent periods of retarded or arrested growth of the scale.
5. Whether the growth of the fish in length is retarded or arrested at the time of formation of the annuli.
6. What factors are responsible for the arrest or retardation of growth in fish and scales.

Considering now the first three propositions listed above, it is believed that the first two are fairly well established and that the last one forms the crux of the whole problem. If the age of a fish can be determined with certainty, the establishment of the validity of the third proposition becomes a comparatively easy matter in a group of fishes whose scales show growth rings. Indisputable evidence of a correlation between the number of annuli on the scales and that of the years of life of their bearer can only be obtained by observation on fish of known age in the field and in the laboratory. And the value of the results rises with the number of years for which this correlation is found to exist.

An extended review of the literature is reserved for a later paper. Here I indicate briefly the chief differences of viewpoint.

Both Hoffbauer (1898, 1899, 1901) and Walter (1901) believed that the age-hypothesis does not hold for carp older than four years. Likewise Brown (1904) and Tims (1906) contradicting Thomson (1904) held the scale method entirely unreliable as applied to the Gadidae. Even Thomson concludes from his experiment that a well-fed whiting may pass the winter without forming an annulus on its scales. Arwidsson (1910) concludes from his study of a series of salmon, 4 to 36 months old, that the completion of the first annulus does not occur at a definite time of the year nor at a definite age, but only at a definite length of the fish, viz., at 60 mm. Masterman (1913) asserts that it is a well known fact that the otoliths or "ear-stones" often used for age-determinations cease growing in the plaice after 6 or 7 years, and that scales also are unreliable after the first 4 or 5 years, though the latter statement is questioned by Hutton (1914). Likewise Scott (1906) expresses the opinion that otoliths do not show the exact age of their possessors. Many other authors may be quoted as opposing the age-hypothesis, but an overwhelming majority assume the validity of the theory and apply it.

Much diversity of opinion exists as to the relation between the formation of annuli and the growth of scales and body. The majority of students believe that the annuli are due to seasonal variation in body growth, that they correspond to retarded growth; but Cunningham's (1905) observation and Cutler's (1918) experiments contradict this view in part, while Taylor (1916) denies such a correlation entirely.

Much controversy also obtains relative to the factors governing the formation of annuli. According to Hoffbauer (1898, 1899), Thomson (1904), Fraser (1917) and others food is the primary factor and not temperature. Taylor (1916) and Cutler (1918) conclude from their experiments that food is not the factor involved. Fraser (1917) holds that neither salinity nor density nor temperature has any factorial significance, while Cutler (1918) believes that temperature alone is causative. Rich (1920) refers to the factor as "a changed environment," Jacot (1920) calls it "migration," while in the case of some trout and salmon the later annuli correspond to a spawning and consequently are transformed into "spawning-marks."

Masterman (1913) wrote, "Experience shows that each species of fish must be investigated separately by the method best suited to it," implying that the establishment of the validity of the hypothesis for one species does not necessarily make it applicable to other species of fish.

The scales of the whitefish *(C. clupeaformis)* have never been critically studied. During the course of an extended investigation of the scales of the Coregonine fishes of the Great Lakes, the writer was fortunate in obtaining scales of this species of known age—nine years. This material forms the basis of an attempt to test the underlying assumptions of the scale method of computation as applied to this species. It also is believed to throw light on the relation between annuli and rate of growth; while the accompanying data permit a discussion of the environmental factors involved in annulus formation.

Here I wish to present a brief description of the apparatus used for the measurement of scales, as my method differs from those ordinarily employed. The instrument is constructed on the principle of a photomicrographic apparatus in which the image is projected on the ground glass. The apparatus consists of a rectangular wooden frame, 14 inches square and 34 inches long. Into one end of the frame is fitted, flush with the exterior surface of the frame, a piece of ground glass, 12 inches square. A tapering bellows made of ordinary chart cloth painted black is attached to the ground glass end of the frame. The bellows when fully stretched extends about three-fourths the length of the wooden frame. The tapered end of the bellows is attached to a small square wooden frame into which is tightly fitted a wooden block in the center of which a hole large enough for the insertion of the microscope tube is bored. When the apparatus is used in the vertical position the microscope is simply placed beneath and extended into the bellows. It is much easier to use this instrument in the horizontal position. In this case the microscope stand is attached to a board at the base of the wooden frame (the end opposite that into which the ground glass is fitted) and the microscope tube drawn into the horizontal position. The open base of the frame is then covered with a sheet of black paper into which a hole is cut so as to allow the light to enter the condenser of the microscope. A special Bausch and Lomb lamp with a 108-Watt bulb furnishes the illumination and is placed about two feet from the base of the frame. A special aspherical condenser accompanying the special lamp is used in the place of the ordinary condenser. The light concentrated upon the hole in the black paper passes through the condenser, microscope tube and bellows, and projects the scale upon the ground glass.

A mechanical stage is always used. To each adjustment button of the mechanical stage is attached, by means of a universal joint cut from a piece of tin, slender wooden rods which extend a little beyond the ground glass end of the frame. In a similar way another rod is attached to the coarse adjustment screw of the microscope. By means of these rods the scale can be moved into place and properly focused from the ground glass end of the frame. The projected scale is measured with an accurate wooden or transparent millimeter rule which is held in place against the ground glass by two strips of steel, four of which are screwed on the wooden frame, one at each corner. To facilitate the counting of the circuli of each scale an ordinary reading glass is used. The whole apparatus is placed upon a long table and may be covered with a black cloth. No dark room is required as the lamp is strong enough to project a clear image on the ground glass in a room illuminated by electric lights; during the day the curtains of the room must be drawn.

The advantages of this method of scale reading over those which use the camera lucida, ocular micrometer or micrometer eyepiece are many. In the first method the scales can be highly magnified without any part being lost to view as is the case in the microscope tube; the circuli and the distances between the annuli of such highly magnified scales can be more accurately, more quickly, and more easily enumerated and measured; and, if the illumination is properly adjusted, scale work can be done with much less straining of the eyes.

When the apparatus is used in the horizontal position it is necessary that the scales be mounted in a stiff medium. Each scale is therefore cleaned in water with a small bristle brush and mounted in a medium of glycerine to which has been added filtered gelatine and a little carbolic acid. The glycerine and gelatine are mixed in such proportion that the solution will stiffen immediately upon cooling. When in this medium, the scales can be stored as permanent mounts and can also be photographed. The photomicrographs (Figs. 137-142) are of scales mounted in a gelatine-glycerine solution.

I wish to express my appreciation to Dr. Charles H. Townsend, the Director, and to Miss Ida M. Mellen, the secretary and scientific assistant of the New York Aquarium, through whose kindness and efficient cooperation I have been able to obtain the whitefishes and scales for this work. These whitefishes, the only ones known to have been reared in captivity, form a valuable exhibition at the Aquarium so that it has been no small sacrifice to part with even a few of them. I am also indebted to Dr. Walter Koelz of the U. S. Bureau of Fisheries who has kindly given me access to his field data and manuscript on the Coregonine fishes of Lake Huron. I would further express my obligations to Prof. Jacob Reighard, who read the manuscript and generously gave assistance in the course of the work. To Mrs. Alvina M. Woodford, of the University of Michigan Library, I am indebted for many valuable suggestions relative to the photographing of the scales.

NEW YORK AQUARIUM WHITEFISH SCALES

Annuli and Number of Winters of Life

Twenty-seven preserved specimens of the Aquarium whitefish, hatched January, 1913, were received. These had died (or had been killed) at intervals between August 13, 1920, and January 3, 1922, as shown in Table I—a period of sixteen months. The fish received had died (been killed) during every month of the year except November. The lengths of each specimen at the time of death is shown in column K of Table I and is followed by the formula which indicates the sex and the condition of the sex organs (see p. 403). The remaining entries in Table I are calculated values and will be referred to in another place.

Table I—Showing for 27 New York Aquarium Whitefish hatched January, 1913, from eggs from Put-in-Bay Hatchery, the U. of M. Museum number, the date of death, the length in mm. (K) at time of death (measured snout to caudal), the sex and condition of sex organs, the lengths in mm. at the end of each winter of life as calculated from the scales (K_1, K_2, K_3, etc.), the annual growth increments in mm. as determined from scales (k_2, k_3, etc.), and the averages of these calculated values for each year of life. Below the calculated averages at the bottom of the columns are given the average lengths and average annual increments for each year of 238 Lake Huron whitefish as determined by actual measurements; the average length of the first year, however, is based on diameter measurements of scales, as no one-year-old whitefish were available.

U. of M. Museum Number	Date of Death	Length in mm. K	Sex and Stage of Organs*	K_1	K_2	K_3	K_4	K_5	K_6	K_7	K_8	k_2	k_3	k_4	k_5	k_6	k_7	k_8	k_9
54505	Aug. 13, 1920	227	♂ D	55	97	110	142	167	190	217		42	13	32	25	23	27	10	
54506	Oct. 26, 1920	245	♂ D	58	136	152	176	206	218	236		78	16	24	30	12	18	9	
54507	Dec. 1, 1920	265	♂ D	65	131	161	183	210	233	256		66	30	22	27	23	23	9	
54508	Dec. 30, 1920	287	♀ A1-2-4E	108	175	199	219	234	256	274		67	24	20	15	22	18	13	
54509	Jan. 28, 1921	219	♀ A1-2-3D-	63	113	127	143	163	190	206		50	14	16	20	27	16	13	
54510	Feb. 28, 1921	334	?eviscerated	112	201	234	255	277	299	314		89	33	21	22	22	15	20	
54511	Mar. 4, 1921	303	♀ A3D-	67	135	156	196	222	253	280		68	21	40	26	31	27	23	
54512	Mar. 28, 1921	286	♀ A4D-	66	156	181	211	229	247	263		90	25	30	18	18	16	23	
54513	Apr. 28, 1921	278	♂ E	70	149	176	202	219	233	250	274	79	27	26	17	14	17	24	4
54514	May 28, 1921	210	♀ A2D-	43	92	109	128	157	179	193	203	49	17	19	29	22	14	10	7
54515	June 25, 1921	275	♀ A2-4D-	49	120	155	189	201	219	241	256	71	35	34	12	18	22	15	19
54516	July 13, 1921	282	♀ A5D	81	136	159	180	198	217	240	259	55	23	21	18	19	23	19	23
54517	July 27, 1921	310	♂ C	69	150	175	208	232	250	270	291	81	25	33	24	18	20	21	19
54518	July 27, 1921	311	♂ E	51	134	182	216	244	262	278	296	83	48	34	28	18	16	18	15
54519	July 28, 1921	256	♂ E	72	120	166	179	205	228	238	248	48	46	13	26	23	10	10	8
54520	July 28, 1921	268	♀ D	67	119	168	188	206	232	245	263	52	49	20	18	26	13	18	5
54521	July 28, 1921	322	♂ C	62	182	199	217	247	271	287	309	120	17	18	30	24	16	22	13
54522	Aug. 3, 1921	287	♀ A3-4-5D+	66	126	149	166	185	204	232	270	60	23	17	19	19	28	38	17
54523	Aug. 3, 1921	339	♂ D	91	116	207	235	261	278	299	319	25	91	28	26	17	21	20	20
54524	Aug. 25, 1921	259	♀ D	51	111	142	175	195	217	232	246	60	31	33	20	22	15	14	13
54525	Sept. 11, 1921	220	♂ C	40	78	114	128	149	163	194	208	38	36	14	21	14	31	14	12
54526	Sept. 18, 1921	275	♀ A6D-	65	113	146	186	199	212	223	247	48	33	40	13	13	11	24	28
54527	Oct. 25, 1921	235	♂ C	71	110	137	168	177	191	214	225	39	27	31	9	14	23	11	10
54528	Dec. 20, 1921	329	♂ A	54	146	205	232	253	271	288	307	92	59	27	21	18	17	19	22
54529	Dec. 20, 1921	320	♀ B	67	131	174	191	213	236	273	295	64	43	17	22	23	37	22	25
54530	Jan. 3, 1922	317	♂ C or A	50	128	183	217	252	265	280	299	78	55	34	35	13	15	19	18
54531	Jan. 3, 1922	347	♀ B	84	154	193	232	256	278	305	332	70	39	39	24	22	27	27	15
	Length and increment averages of N. Y. Aq. whitefish.			67	132	165	191	213	233	253	271	65	33	26	22	20	20	18	
	Length and increment averages of 238 Lake Huron whitefish.			119?	213	268	322	366	412	449		94?	55	54	44	46	37		

*For explanations of the letters denoting the stage of sex organs, see p. 403. Also see Table VII.

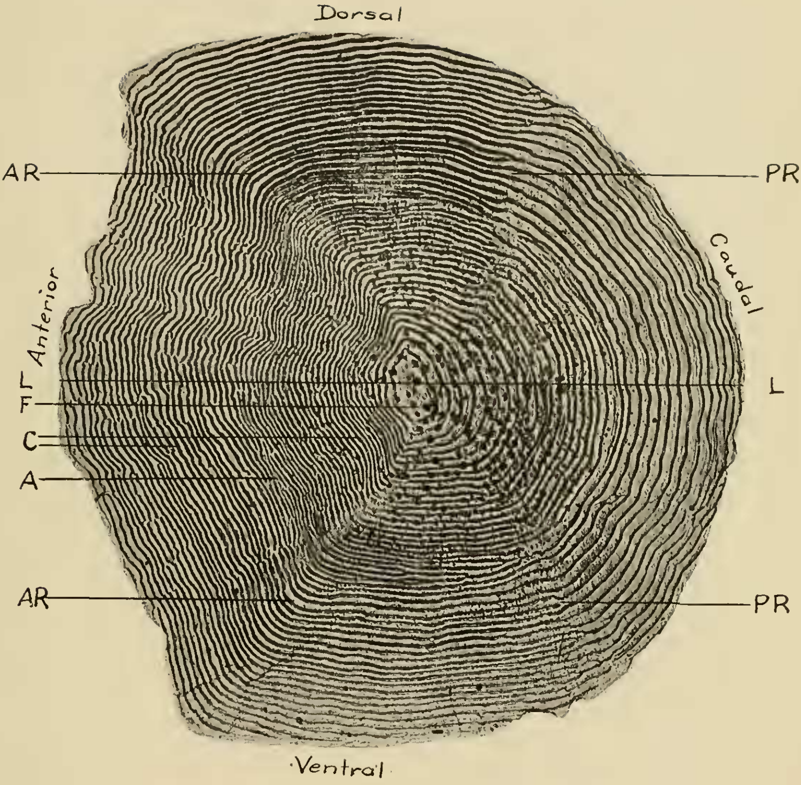

FIG. 137. Typical scale of Lake Huron Whitefish *(Coregonus clupeaformis* Mitchill) from East Tawas, Michigan. Length of fish, 197 mm., captured October 22, 1917. L-L, length of scale; F, focus; C, circuli; A, annulus of first winter; AR, antero-lateral ridges; PR, postero-lateral ridges; Dorsal, Ventral, Anterior, Caudal border and area. X-25.

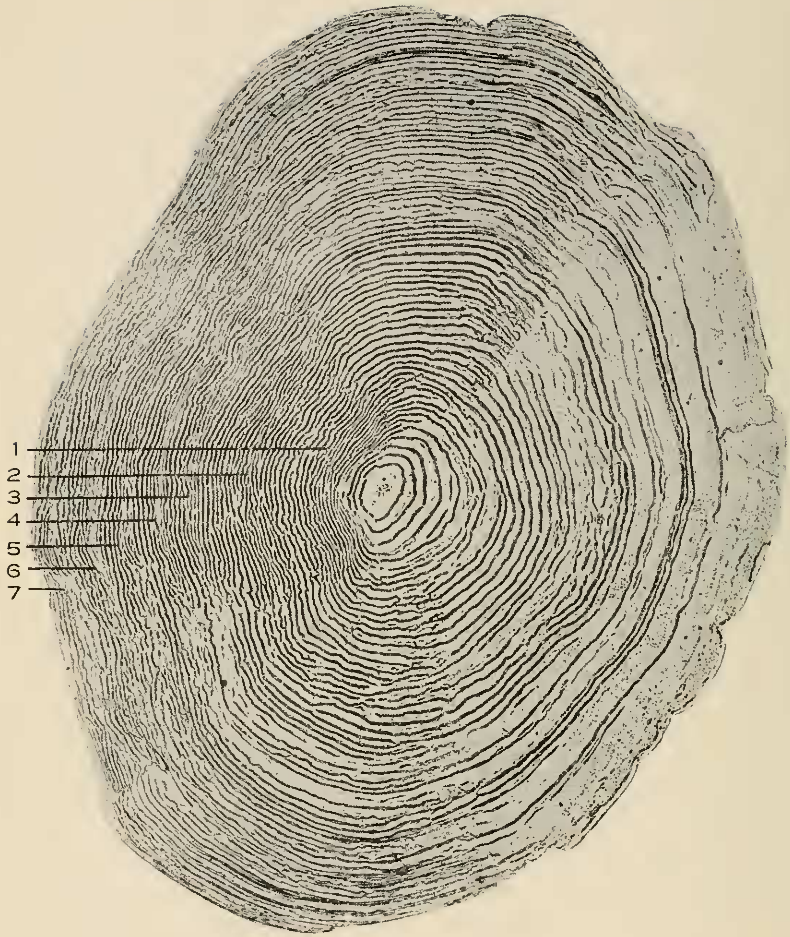

FIG. 138. Scale of New York Aquarium Whitefish *(C. clupeaformis)* hatched January, 1913; killed December 1, 1920. U. of M. Museum No. 54507; Male, 265 mm. long, 7 years, 10 months old. Scale shows 7 completed annuli and a marginal growth. X-22.

Fig. 139. Scale of New York Aquarium Whitefish *(C. clupeaformis)* hatched January, 1913; killed April 28, 1921. U. of M. Museum No. 54513; Male, 278 mm. long, 8 years, 3 months old. Scale shows 8 completed annuli, the eighth at the margin. X-18.

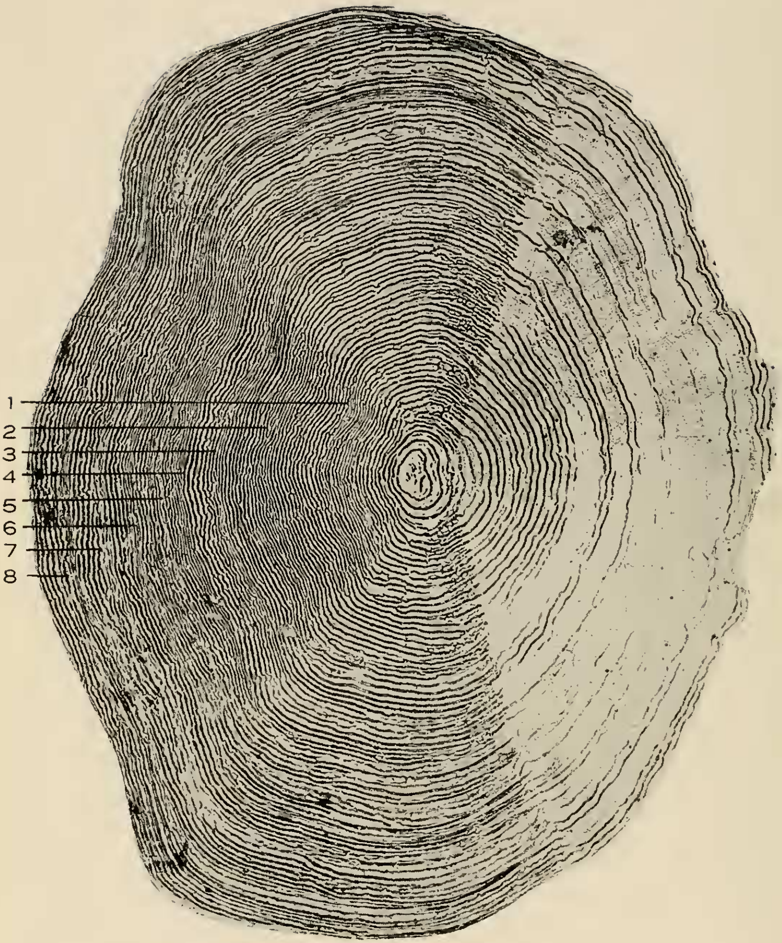

FIG. 140. Scale of New York Aquarium Whitefish *(C. clupeaformis)* hatched January, 1913; died July 13, 1921. U. of M. Museum, No. 54516; Female, 282 mm. long, 8 years, 5½ months old. Scale shows 8 completed annuli and a marginal growth. X-18.

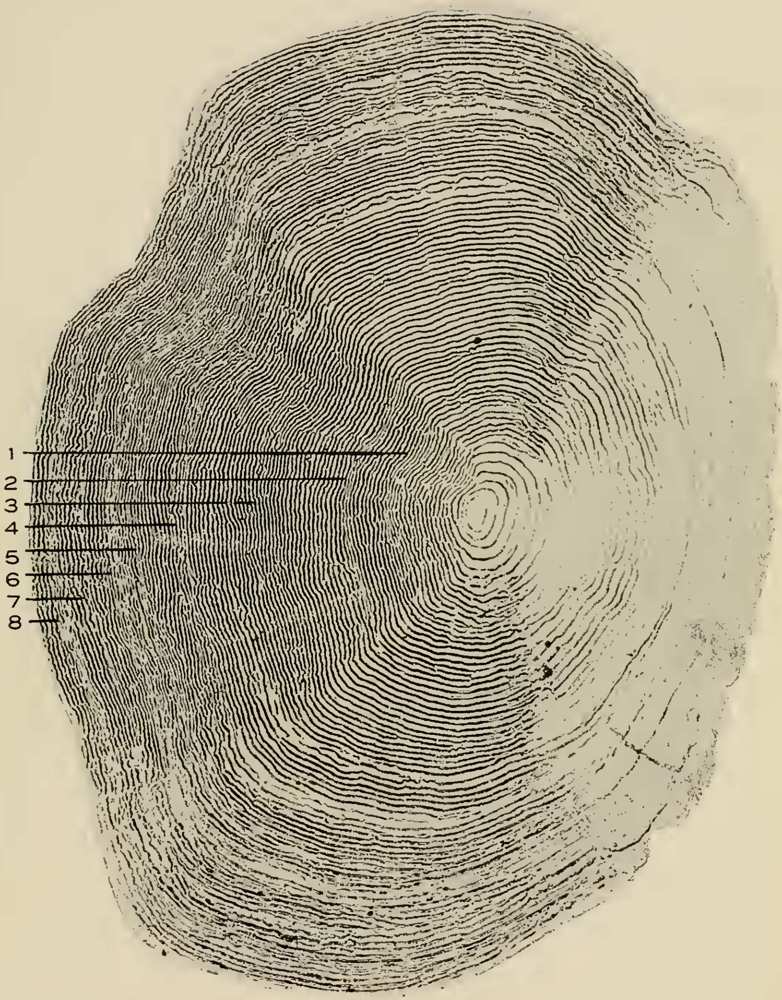

FIG. 141. Scale of New York Aquarium Whitefish *(C. clupeaformis)* hatched January, 1913; died August 3, 1921. U. of M. Museum No. 54523; Male, 339 mm. long, 8 years, 6 months old. Scale shows 8 completed annuli and a marginal growth. X-16.

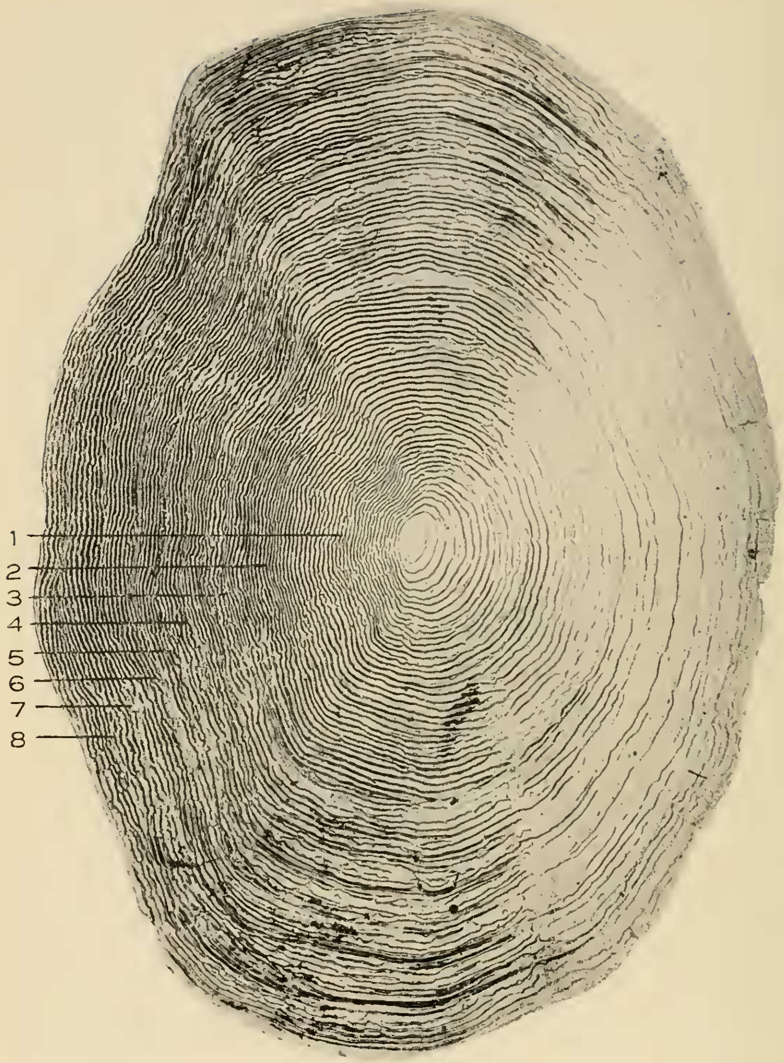

FIG. 142. Scale of New York Aquarium Whitefish *(C. clupeaformis)* hatched January, 1913; died January 3, 1922. U. of M. Museum No. 54531; Female, 347 mm. long, 9 years old. Scale shows 8 completed annuli and a marginal growth. X-19.

Figs. 138-142 are photomicrographs of scales taken from Aquarium fish killed at different ages. On each photograph reference lines have been drawn which indicate the positions of the annuli of the different years. On comparing the scales of these aquarium whitefishes with those of the wild whitefish, it may be seen that the former are much stunted in growth; their circuli are more irregular and crowded together, while their annuli, in some instances, nearly come into contact in the posterior or exposed area of the scale. In some scales the annuli are difficult to observe, but by the use of various magnifications and by the manipulation of the light source they can be determined. In most of the fish several scales are necessary for an age-determination. I gradually discovered, however, that those aquarium scales whose caudal area is longer than its anterior area and whose form approaches the elliptical possess annuli that can be more readily determined than those of scales without these characters. Such scales were usually obtained from the area between the pectoral fin and the lateral line. Those photographed and employed in this study were taken from the left side of the body.

The first specimen died August 13, 1920, at the age of seven years and seven months. Its scales possessed seven annuli with a small amount of marginal growth. The number of annuli, thus, corresponded with the number of years of life of the individual. The next seven specimens received (54506 to 54512, Table I), which ranged from seven years and nine months to eight years and two months in age, also possessed scales with seven completed annuli and various amounts of marginal growth. Fig. 138 represents a photograph of a scale from the specimen killed December 1, 1920, and shows seven annuli with the eighth year increment at the margin. The eighth annulus is completed in April. Fig. 139, a photograph of a scale from the April specimen, shows the eighth annulus situated at the margin. In the remaining eighteen specimens (54514 to 54531, Table I), which ranged from eight years and four months to nine years in age, the eighth annulus is entirely removed from the margin and surrounded with various amounts of the ninth year increment. Figures 140, 141 and 142 are photographs of scales from specimens that died July 13, 1921, August 3, 1921, and January 3, 1922, respectively. Each figure shows eight annuli and, presumably, a completed ninth year's growth.

It thus appears (1) that the specimens received from August, 1920, to March, 1921, which represent ages from seven years and seven months to eight years and two months possessed

Table II—Showing at different dates the average total length in mm. of magnified scales of individuals of whitefish reared in the New York Aquarium; the percentage of the scale length outside the outermost annulus (marginal growth) in the antero-posterior diameter included in the last annulus, the part of this marginal growth percentage formed since the preceding date and the number of scales upon which the averages are based.

U. of M. Museum Number	Name of Fish	Date of Removal of Scale	Date of Death of Fish	V7 or V8 Average Length of Scales at End of 7th or 8th Growth Year	v8 or v9 Average Length of Marginal Growth in 8th or 9th Year	v8/V7 or v9/V8 Percentage Added to Scale Outside Last Annulus	△ Percentage Added Since Preceding Date	Number of Scales on Which Each Average is Based
54507	Crooked-back	Oct. 26, 1920		201	5.8	2.8*	+2.8*	4
		Nov. 26, 1920		167	3.7	2.2	—0.6	3
		Dec. 1, 1920	Dec. 1, 1920	175	5.2	2.9	+0.7	5
54516	Double-crook	Dec. 30, 1920		185	16	8.6*	+8.6*	1
		Feb. 25, 1921		183	16.5	9.0	+0.4	2
		April 26, 1921		220	5	2.2z	+2.2z	2
		June 29, 1921		221	16	7.2	+5.0	3
		July 13, 1921	July 13, 1921	189	14	7.4	+0.2	4
54515	Open-gill	Jan. 26, 1921		175,	12.5	7.1*	+7.1*	2
		March 26, 1921		199	13.3	6.7	—0.4	3
		May 26, 1921		221	15.6	7.0z	+7.0z	3
		June 25, 1921	June 25, 1921	183	16.6	9.0	+2.0	6

* Since March or April, 1920.

z 1921 growth.

scales with seven annuli and various amounts of marginal growth and therefore belong to the same growth year, the eighth, even though the three fish received from February to March actually were in their ninth year of life; (2) that those received from April, 1921, to January, 1922, which vary from eight years and four months to nine years in age possessed scales with eight annuli and different amounts of marginal growth.

The annuli are thus actually proved to be of the same number as that of the winters of the fish's life, if we exclude the first one in which the fish was hatched.

Marginal Growth and Time of Formation of Annuli

Two specimens of the aquarium fish were segregated in the New York Aquarium and kept living with the purpose of taking scales from them at monthly intervals in order to follow the seasonal changes in the scales from November until June. Owing to deaths a total of six fish was employed during this interim, three of which lived for periods of two, six and seven months. In Table II these fish are designated by names indicating slight physical peculiarities and by their museum numbers. The names should not be taken as indicating that the fish were notably deformed. They were the smaller, poorer fish, less desirable for exhibition purposes. Table II shows the average total length in mm. of the magnified scales taken from these fish in different months, the average total length in mm. of the marginal growth, the percentage of its length in the antero-posterior diameter of that part of the scale included in the last annulus, the difference in the percentages of successive months and the number of scales upon which each average is based. The percentages in this table are, however, only approximately correct as they vary with the areas on the body of the fish as well as with the scales taken from the same area. However, as all the scales, except those removed from the dead fish, have been taken from the same area, the variability of the scale values has been reduced to a minimum so that they may be used with confidence in drawing certain conclusions.

The discrepancy in the fall or winter percentages (which seem to show scale absorption) of Crooked-back and Open-gill are presumably due, then, to the variability of their scales. The small difference (+0.4) between the two winter percentages (8.6 and 9.0) of Double-crook which represent a period of two months, likewise may be looked upon as due to this same variability and thus can have no significance. Presumably, then, the percentages in column v8/V7 or v9/V8 remain constant for

Table III—Showing for all New York Aquarium fish of Table I the percentage of the scale increment of the 7th, 8th and 9th year in the total scale length of the 6th, 7th and 8th year respectively and the average for each series of percentages.

Date of Death	v7/V6 Percentage of 7th Year Increment in Scale Length of 6th Year	v8/V7 Percentage of 8th Year Increment in Scale Length of 7th Year	v8/V7 or v9/V8 Percentage of Incompleted 8th or 9th Year Increment in Scale Length of 7th or 8th Year respectively	Number of Scales on Which Percentages Are Based
August 13, 1920	14.5		4.7	2
October 26, 1920	8.2		4.1	2
December 1, 1920	9.8		2.9	5
December 30, 1920	7.4		4.7	2
January 28, 1921	8.8		6.2	2
February 28, 1921	5.2		6.4	2
March 4, 1921	10.9		8.5	2
March 28, 1921	6.6		8.9	2
			5.8a	
April 28, 1921	7.3	9.3	1.6b	1
May 28, 1921	8.1	5.0	3.4	1
June 25, 1921	9.8	6.5	9.0	1
July 13, 1921	10.8	7.6	7.4	1
July 27, 1921	8.9	7.8	6.5	2
July 27, 1921	5.9	6.5	5.2	1
July 28, 1921	4.5	4.3	3.0	1
July 28, 1921	5.6	7.4	2.0	1
July 28, 1921	5.9	7.5	4.3	1
August 3, 1921	13.4	16.3	6.1	1
August 3, 1921	7.3	6.8	5.6	1
August 25, 1921	7.1	5.7	5.4	1
September 11, 1921	18.8	7.3	5.7	1
September 18, 1921	5.2	10.8	11.5	1
October 25, 1921	12.0	4.9	4.6	1
December 20, 1921	6.3	6.8	7.1	1
December 20, 1921	15.8	8.2	8.4	1
January 3, 1922	5.9	6.5	6.1	1
January 3, 1922	9.8	8.9	4.5	1
Average =	8.9	7.6	6.5c	

a—Average for incompleted 8th year, August to March. b—Ninth year increment begins.
c—Average for incompleted 9th year, August to January.

each fish during the fall and winter, *i. e.*, the marginal growth of the scales is arrested during the period from October to March. Marginal growth is resumed sometime in April (or March?). On April 26, 1921, the new marginal growth of Double-crook showed a percentage of 2.2, which value was increased to 7.4% on July 13, two and one-half months later. Similarly, Open-gill showed a new marginal growth of 7.0% on May 26, 1921, which percentage was increased to about 9.0 on June 25, one month later. The percentages of Double-crook and Open-gill are thus entirely consistent with and comparable to each other from April on and show that rapid scale growth is resumed sometime in April (or March?) and is continued at least until July.

In order to show approximately by comparison how much of the new year's growth was completed by Double-crook and Open-gill at the time of death, I computed percentages, similar to those of Table II for the preserved specimens listed in Table I. Table III shows in column v7/V6 the percentage of the scale increment of the seventh year in the total length of the scale included in the sixth annulus, in column v8/V7 the percentage of the scale increment of the eighth year in the total scale length included in the seventh annulus, and in column v8/V7 or v9/V8 the percentage of the incomplete marginal growth of the eighth or ninth year in the total scale length included in the last completed annulus (7th. or 8th.). The average for each series is given at the bottom of each column.

From this table it may be seen that the average percentage of the completed seventh year scale increment in the total scale length of the sixth year for 27 specimens is 8.9 and somewhat less, as is to be expected, for a similar percentage for the next year (7.6) for 19 fish. When these averages (8.9 and 7.6), which represent the completed seventh and eighth growth years are compared with the percentages of Double-crook and Open-gill (7.4 and 9.0) and when it is remembered that the percentage for the ninth year may reasonably be expected to be somewhat less than that for the eighth, it may safely be assumed that the scales of the segregated fish have just about completed their ninth year's growth and certainly would have done so by August or September.

If we now assume that August closes the period of scale growth and compute the average of the percentages of the incomplete ninth year from August to January and compare this average with those of the two preceding completed years and with the percentages of the two segregated fish we may obtain a criterion which ascertains roughly the probability of the correctness of our assumption relative to the time of the cessation of scale growth. Table III shows that such a ninth year average is 6.5%, which compares favorably with those of the two preceding completed years (8.9 and 7.6), and may therefore be considered as representing the average of a completed ninth year. The ninth year average (6.5) thus suggests the completion of scale growth by August not only in the fish of Table II (with 9th year percentages of 7.4 and 9.0), but also in those of Table I. Again, when the average of the percentages of the incomplete eighth year from August to March is compared with that of the completed eighth year, it is found that the former (5.8) compares fairly well with the latter (7.6) when it is remembered that the fish sacrificed first (included in the 5.8 average) were the poorer and less valuable specimens. Thus again scale growth may presumably be considered complete by August. Also, Tables II and III show that the percentages of the incomplete eighth and ninth years show no consistent increase from August and October to April, while those of the ninth year from April to June or July do.

In the light of the preceding discussion it now appears reasonable to accept the interpretation presented on page 391 relative to the constancy of the fall and winter percentages given in Table II.

Table III, column v8/V7 or v9/V8, further corroborates Table II and shows that marginal growth is resumed in April. All the fish killed after April, 1921, completed the new annulus and showed various amounts of new marginal growth on their scales.

The percentages of Table II show, then, (1) that there was no marginal growth present in November and December of 1920, and in January, February and March (?) of 1921, and, (2) that a new annulus was recognizable in April, 1921, and was correlated with a resumption in scale growth. The percentages of Table III corroborate the conclusions based on Table II, and in addition show in conjunction with Table II that marginal growth was presumably arrested by August in 1920 and 1921, and certainly by September. The data of both tables (II and III) therefore prove that the annulus is a winter-mark due to a retardation or cessation of scale growth and is completed upon the resumption of rapid scale growth in the spring of the year.

Table IV—Showing for 76 Alpena whitefishes collected September, 1917, the relation of the average length of the diameter (v), anterior (ac) and posterior (pc) radius of the scale to the average body length (K), all lengths expressed in mm., for fish in years III to VII inclusive.*

In Year	III	IV	V	VII
K	269 (47)	315 (14)	352 (9)	456 (6)
v	5.75 (47)	6.75 (14)	7.49 (9)	9.58 (6)
ac	3.19 (47)	3.86 (14)	4.34 (9)	5.80 (6)
pc	2.56 (47)	2.89 (14)	3.15 (9)	3.78 (6)
K/v	46.78	46.67	46.99	47.60
K/ac	84.33	81.61	81.11	78.62
K/pc	105.08	108.99	111.75	120.63

*Numbers in parentheses following averages indicate the number of specimens employed; the sixth age-group contains only one specimen, therefore, omitted.

Correlation Between Annual Growth in Length of Body and Scales

It now remains to examine for the whitefish the correlation between the annual increment in length (or other dimension) of scales and length of body. Had it been possible to measure the body lengths of the living aquarium whitefish accurately at the time of the removal of their scales, this correlation could have been established by direct observation. Obviously, Table I does not afford material for this purpose as the number of specimens received each month is too small to warrant valid averages of monthly growth increments in body and scales. The available aquarium whitefish therefore cannot show the proportionate growth of body and scale.

Wild whitefishes may be used to show this correlation. In this case it is necessary that a large amount of strictly homogeneous material be used, *i. e.*, the fish of the several age-groups must all belong to the same race and have similar rates of annual growth increments, and only scales from corresponding body areas must be employed. These requisites necessitate the acquisition of a large collection of fish taken at the same time and at the same locality. At present no such whitefish material is available. There are, however, at hand, series of body and scale length measurements of a small collection (76 fish) of Lake Huron whitefishes taken September, 1917, at Alpena, Mich. A summary of their data is given in Table IV.

In row K, Table IV, is shown the average length in mm. of the fish of each age-group, the age-group referring to the year of life in which the fish were captured. The number of specimens in each age-group is shown in parenthesis. In row (v) is given the average length in mm. of the scale diameters of the fish of each age-group. In rows (ac) and (pc) the same averages are

Table V—Showing for each year for Alpena whitefish (Table IV) in the seventh year the average length in mm. calculated from the diameter (v), anterior (ac) and posterior (pc) radius of scales (Table IV), and the difference between the calculated averages and those of the age-groups obtained from actual measurements (K).

	III	IV	V	VII
K	269	315	352	456
Calculated (K) from (v)	274	321	357	
Calculated (K) from (ac)	251	303	341	
Calculated (K) from (pc)	309	349	380	
Difference (K) & (K from v)	+5	+6	+5	
Difference (K) & (K from ac)	—18	—12	—11	
Difference (K) & (K from pc)	+40	+34	+28	

given for the anterior and posterior radius of the scale respectively. In the last three rows are shown the body-scale ratios for each age-group based on the diameter (v), anterior (ac) and posterior (pc) radius respectively.

The number of fish in each age-group is not as large as one could wish, but may be sufficiently large to show roughly the relation of the length of the various scale dimensions to body length. It may then be seen that the K/v ratio is about the same for the third and fourth age-group and rises slightly in the fifth and again in the seventh. This means that the diameter increases in length in a simple proportion to the increase in the length of the body during the fourth year and increases at a slightly slower rate relative to the body in the fifth and seventh years and presumably also in the sixth for which no values can be given. The K/ac ratio is found to decrease with age, while the K/pc ratio increases with age. This means that the anterior radius of the scale grows faster relatively than the body with age, whereas the posterior radius grows more slowly with age. None of the measured scale dimensions therefore grow strictly proportionate to the body.

In order to show roughly in a practical way which dimension most nearly acquires this proportionate growth and furnishes the most accurate estimated length values, I calculated the average length for each year of the fish in the seventh year, using the average scale dimensions of Table IV. The estimated lengths are shown in Table V. From this table it may be seen that there is a high degree of correspondence between the lengths calculated from the diameter and the actual lengths, and that the former are somewhat higher than the latter. The lengths calculated from the anterior radius are lower, while those calculated from the posterior radius are much higher than the actual lengths. It is, however, realized that these calculated and actual values may not be strictly comparable as the two series of values represent different year-classes which may have varied considerably in their rate of growth. Strictly, series of fish of the same year-class collected in the same season of different years and at the same locality are required for an absolutely valid check on calculated values.

Table V also shows that the calculated values from diameters are consistently found between those based on the radii. This was also found to be true for the individual fish. Experience has shown that in practically every species of fish whose scales were studied the calculated values based on radii (no other dimension is ever used) and checked with the actual values were always found to be too low for the early years of life. The Coregonines prove to be no exception. In the light of past experience therefore, and in view of the fact that diameter measurements of whitefish scales raise the calculated values, especially those for the earlier years, above those based on the anterior radius, it may be deemed advisable to test the various dimensions of the scales, where possible, before undertaking any extensive scale work for a species.

Tables IV and V show for the whitefish (1) that the diameter, anterior and posterior radius of scales increase in length at very different rates with respect to the rate of increase in the length of the body and that consequently the calculated length values based on the different scale dimensions vary significantly, (2) that none of the three scale dimensions considered increase in length at a rate strictly proportionate to the rate of increase in length of the fish, (3) that, presumably, the diameter of the scale increases in length at a rate more nearly proportionate to the rate of increase in body length than either the anterior or posterior radius and therefore should be used for the calculations of length values, and (4) that the calculated values based on the diameter always lie between those based on the anterior and posterior radii.

Life History of the Aquarium Whitefish and the Factors of Annuli Formation

In view of the great diversity of opinion among investigators, and in view of the disagreement and contradiction of the conclusions reached by various authors from laboratory experiments and field observations relative to the factors responsible for the formation of annuli, it was deemed advisable to obtain as complete a life history as possible of the New York Aquarium whitefishes and thus, perhaps, determine to a certain degree the relative significance of each environmental factor in the formation of annuli. It is realized that these life history data are not equivalent to those of carefully planned and executed series of experiments in which only one factor of the environment is altered at one time and the results checked with those of a control. Yet, it will be seen that experimental requirements are partly fulfilled for the fish were regularly supplied with food in amounts controlled by their appetites, while the temperatures varied from those of summer to those of winter and vice versa. And as the period of rapid scale growth and the time of the formation of an annulus are known the effect upon the scales of a change in a factor may be approximately ascertained. I am indebted to Miss Mellen and to Mr. Robert J. Lanier, who reared the whitefishes, for most of the life history data. I alone am responsible for the conclusions derived from them.

It has now been proved (p. 394) that the formation and completion of an annulus is dependent upon the retardation or cessation and resumption of scale growth, and that scale and body growth are closely correlated; therefore, any factor that can affect the growth rate of the body may have primary significance in the formation of an annulus. But to hold such a factor responsible it must be established that a change in this factor occurred previous to or synchronously with the change in the rate of growth and that no resumption of rapid scale or body growth can occur until the change in the factor is reversed or its effectiveness lost. The primary factors may be different from year to year or even from season to season in the same year.

(a) Food

The Aquarium whitefish were fed in about the same way throughout the year. Miss Mellen writes: "I have consulted our superintendent (Mr. Robert J. Lanier), who reared the whitefishes born in 1913, as to their food since hatching, and find that in early infancy they had the advantage of some live food, receiving first herring roe, next a few mosquito larvae, third, the fry of pike perch, which happened to be hatching at just the right time, although all would not take this food, as, unlike most fishes, they do not normally eat their own kind, and lastly, minced beef-heart. Feedings were very frequent during the first couple of years, after which they were fed daily on beef-heart. From 1915 to 1918 inclusive they were fed exclusively on beef-heart three times a week; and it is only since 1919 that they have been fed with beef-heart exclusively three times a week in summer and beef-heart once, clam twice a week in winter."

The amount of food, however, actually consumed by the fish varied somewhat with the seasons. In the earlier years when the fish were fed daily, Mr. Lanier gave them less food during January, February and March in spite of the fact that they were always ready to eat. During their third year an apparent change in their appetites occurred, so that thereafter they were fed only three times a week. Since this year (1915) it was also noticed that the fish "did not eat quite as much during January, February and March," though the number of feedings remained constant throughout the year.

It is obvious that since the character of the food and the number of feedings remained constant summer and winter for several consecutive years these factors could not have altered the rate of scale or body growth. The amount of food, however, offered or taken by the fish, did vary with the season. How much the amounts varied is not known. In the fall of 1920 this change in the amount of food could not have had any significance inasmuch as scale growth was arrested before January, 1921, when this factor was first altered. In April, 1921, the rations were increased for the same reasons that they were decreased in January, viz.—a change in the appetites of the fish. It was previously shown that scale growth was resumed in March (?) or April (p. 393). It thus appears that food and growth are correlated in April, 1921, but in this case the former is presumably only of secondary importance. As nothing definite is known about the distribution of growth in the other years of life of these fish, the relative significance of food as a factor in these years can only be conjectured and therefore requires no discussion here.

(b) Temperature

Table VI shows the monthly and yearly mean temperatures in degrees, Fahrenheit, of the fresh water entering the New York Aquarium, from 1913 to 1920, inclusive. As soon as the water reached a temperature of about 60°F (15.6°C) in the summer, it was refrigerated and maintained at a temperature which varied from 54° to 57°F and averaged about 55°F (12.8°C), except during the summer of 1921, when the range was changed to 50° and 54°F, and the average reduced to about 52°F (11.1°C). The months in which the refrigerating plant was started and stopped are indicated by the letters r and s respectively in Table VI. In Fig. 143 are plotted a curve (T) based on the average monthly temperatures of Table VI and growth curves of the scales of Double-crook (D) and Open-gill (O)

Table VI—Record in degrees, Fahrenheit, of Monthly and Yearly Mean Temperatures of Fresh Water Entering the New York Aquarium, from 1913 to 1920, inclusive.[a]

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Averages
1913	43	41	42	50	....	....r	67	71	70	65	56s	48	55
1914	41	38	40	45	53r	60	67	71	70	65s	54	43	54
1915	39	38	40	47	53r	59	65	69	70	63	54s	42	53
1916	38	37	36	43	52r	56	64	69	69	63	55s	45	52
1917	37	36	39	44	50	57r	62	65	64	58s	49	39	50
1918	35	37	39	44	55	56	58r	64	66	59s	52	42	51
1919	39	38	40	45	54r	60	64	67	66	63	54s	43	53
1920	37	37	39	43	51	61r	66	68	67	63	54s	45	53
Monthly Averages	39	38	39	45	53	58	64	68	68	62	54	43	53

a—From daily observations made by Mr. W. J. DeNyse.

r—Refrigerating plant started.

s—Plant stopped; the temperatures do not represent those of the refrigerated water. The temperatures of the refrigerated water averaged about 55° F. every summer, except that of 1921 when it averaged 52° F.

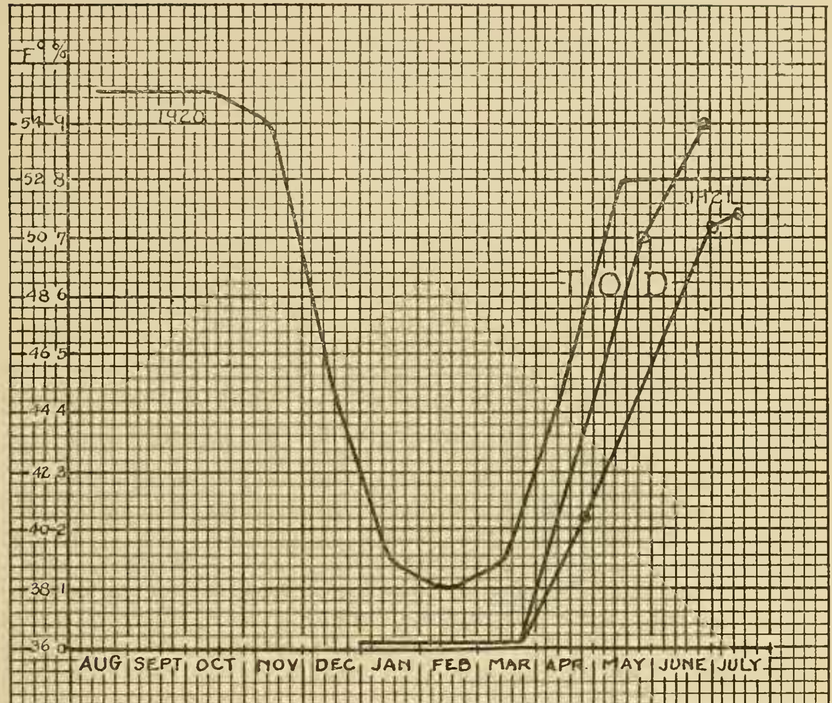

FIG. 143. Showing the relation between the rate of growth of the scales of Open-gill (O) and Double-crook (D) and the temperature (T) of the aquarium water. T-curve based on the average monthly temperatures of the refrigerated and non-refrigerated water shown in Table VI. O-curve based on the percentages of Table II, which represent the total scale growth of Open-gill from March, 1921, to June, 1921. D-curve based on the percentages of Table II, which represent the total scale growth of Double-crook from March, 1921, to July, 1921.

based on the percentages of Table II, which represent the renewed growth of the scale after March, 1921. The growth curves are only approximately correct as the scales of each fish were taken in alternate months.

Fig. 143 shows that the curves of scale growth adhere very closely to the curve of temperature. No growth occurred during the period of low temperatures in January, February and March, and the greatest increase in growth took place at the time of the greatest rise in temperature in April and May. The maximum temperatures were reached in May when the water was refrigerated and maintained throughout the summer at an average constant temperature of about 52°F. Scale growth, however, continued, at least in Open-gill, throughout June. Scale growth therefore was not arrested by the temperatures of the refrigerated water. As these temperatures do not represent those of the water in the whitefish tanks, they may be a little too low, especially those of the non-refrigerated water. This, however, would not alter the general appearance of the temperature curve nor the conclusions based on it..

It is thus seen that scale growth and the temperature of the water are correlated in the spring of 1921, the latter presumably having primary significance. That a low temperature is here a primary factor in growth seems corroborated by the fact that a decrease in the amount of food consumed occurred synchronously with a decrease in temperature and an increase in food consumption with an increase in temperature. The effect of low temperatures upon the metabolism of the body is well stated by Dr. Fulton (1904), who writes (p. 170): "Temperature is active in modifying the rate of growth by acting directly upon the metabolism of the fish and also by affecting the rapidity of digestion. In very cold water the fishes give up feeding altogether, because the ferments upon which digestion depends do not act, or act very slowly, at low temperatures, and in fishes, as in other animals, appetite waits on digestion, and this is, on the other hand, correlated with the metabolism in the tissues. It has been shown by Krukenberg that the pepsine or analogous body in the stomach of fish acts as well at 20°C as at 40°C, at which, among mammals, digestion is most active, and that the rapidity of its action is closely related to temperature; and Knauthe and Zuntz have shown that the same thing applies to the metabolism in fish, the vital activities being more active in the higher temperature, as shown by the excretion of carbonic-acid gas and other products of metabolism."

But, as both food and temperature remained practically constant during the summer until November, what factor must then be held responsible for the arrest in scale growth in August or September? As the aquarium water is well aerated its gaseous content cannot be held responsible; nor could any probable changes in its mineral or salt content account for the decrease in growth. The only remaining variable is sexual maturity.

(c) Sexual Maturity and Spawning

Before attempting to describe the conditions of the ovaries and testes of the various New York Aquarium whitefishes at the time of death, it seems advisable to describe first the normal natural conditions of the sex organs as found in wild whitefishes of various ages. The following description is based on many specimens of Lake Huron whitefishes.

In order to determine the sex of immature wild whitefishes the sex organs must be closely scrutinized often with the aid of a magnifying lens or microscope. This difficulty of determination is due to the fact that the ovaries and testes are quite similar in appearance in the very young whitefishes. Both consist of narrow, thin, flat strands of soft, whitish material and extend from the anterior to the posterior end of the body cavity along its dorsal wall. In the larger immature fish the two kinds of sex organs can be distinguished by their structure. When an ovary is picked up and stretched transverse folds or layers become evident, while the testis under like treatment appears to be a compact homogeneous structure. In still older fish color may also be critical; the ovary becomes yellowish, while the testis retains its whitish color.

In a maturing female the ovary gradually increases in size, the enlargement beginning at the anterior end of the body cavity. Minute round yellowish eggs appear in the ovary folds. At the time of spawning the ovaries have usually enlarged to such extent as to distend and fill the entire body cavity. The condition of the ovary and the size of the eggs thus indicate the stage of sexual maturity in the female. A ripe egg is about 3 mm. in diameter. The maturing testis also increases in size, the enlargement commencing at the anterior end of the body cavity. As the testes grow they extend further into the abdominal cavity and increase in width and thickness. At the time of spawning they nearly fill the body cavity, but usually do not distend it, as do the ovaries. The size of the testes is then a rough index to sexual maturity in the male. When the eggs and sperm are ripe they are easily pressed out of the body. The sex organs of a spent fish are soft and flaccid. This condition is more easily determined for females than for males, and even among the former doubtful cases arise, the magnitude of the doubt depending partly, I presume, upon the length of the interim between the spawning and the date of the capture of the fish.

In describing the various conditions of the sex organs of the New York Aquarium whitefishes I devised a number of phases, each phase indicating rather definite conditions. As the individuals represent nearly every month of the year the conditions of their sex organs intergrade more or less imperceptibly, and it is therefore impossible always to refer a specimen to one phase; parts of different phases may be found in one individual. The ovaries alone permit of a rather definite classification and they only must be considered reliable in a discussion.

The various stages of development[3] are considered under five principal phases designated by the letters A, B, C, D and E as follows:

[3]These descriptions are based on the sex organs of the Aquarium fish preserved in 5% formalin and later transferred to 70% ethyl alcohol.

E: ♀—anterior ¼ of ovary enlarged; eggs microscopic or very small in size.

♂—anterior ¼ of testis enlarged into a flat, white gland; remainder transparent.

D: ♀—anterior ½ of ovary enlarged; ovary flat, rigid, ¾ in. at its widest; eggs of year are round, whitish, easily visible to naked eye, 1 mm. or less in diameter.

♂—anterior ½ of testis enlarged; compact gland thicker and wider than in (E), about ¼ in. at its widest.

C: ♀—entire ovary enlarged; eggs 1-2 mm. in diameter.

♂—anterior ¾ and posterior end of testis enlarged, ½ in. at its widest.

B: ♀—compact ovaries fill body cavity; yellowish eggs nearly ripe, 2-3 mm. in diameter; fish about ready to spawn; body may be pearled.

♂—hard testes fill body cavity; fish about ready to spawn; body may be pearled.

A: ♀—matured eggs retained and in process of absorption. Coincident with this condition is that of (E) or (D), *i. e.,* eggs of the year are evident. Ovaries may be soft, flaccid; retained eggs found either in ovary, in body cavity or in both; eggs average 3 mm. in diameter when round and smooth; eggs are found in various conditions, several of which may be found in one individual; these conditions are designated by number under (A):

1. Eggs hard, round, smooth; each egg partly turned a brownish yellow.
2. Eggs wrinkled, indented, of brownish yellow color; float in water.
3. Eggs wrinkled, indented, peripheral portion of each egg of a dull or dirty transparency; float in water.
4. Eggs flattened, crushed, sometimes a little brown color left; contents absorbed.
5. Eggs with dark reddish color, and a solid, glassy appearance; filled with minute oil globules; eggs about 1 mm. in diameter and scattered among the eggs of the year in a soft ovary; glassy eggs show no evidence of absorption.
6. Ovary soft, flaccid with many eggs of the year, but no retained eggs evident.

♂—testes smaller than in (B); flabby, *i. e.,* fish spent, or testes compact, of reddish color with sex products seemingly retained and undergoing absorption; body may be pearled.

Table VII—Showing distribution in time of the phases of sexual development in the Aquarium whitefish. For explanation of letters and numbers see page 403. Also see Table I.

Month	Females	Males
November	None	None
December	B(20), peduncle pearled; A1-2-4E(30) numerous retained eggs in ovary and body cavity	D(1); A(20) body heavily pearled, testes reddish
January	B(3), abdomen distended; A1-2-3D-(28) retained eggs numerous, mostly in body cavity	C or A(3)
February	None	None
March	A3D-(4) retained eggs numerous, in body cavity; A4D-(28) ½ doz. flattened eggs in body cavity	None
April	None	E(28)
May	A2D-(28) retained eggs numerous, in body cavity	None
June	A2-4D-(25) few wrinkled eggs in ovaries and few partly absorbed ones among pyloric coeca	None
July	D(28); A5D(13) ovary soft, no wrinkled eggs	E(27, 28); C(27, 28)
August	D(25); A3-4-5D + (3) retained eggs numerous, in ovaries and body cavity	D(3, 13)
September	A6D-(18) ovaries flaccid, no retained eggs	C(11)
October	None	D(26); C(25)

The distribution of these phases in time among the aquarium whitefishes is indicated in Table VII. The number in parenthesis following each phase refers to the day of the month on which the specimen died. Each such number represents one individual. The minus or plus sign following a letter indicates an early or a late phase respectively. Two or more phases in one individual are designated by a combination of the proper letters. The phase of each specimen is also shown in Table I.

Table VII shows (1) that no immature female whitefish were received, (2) that two females were ready to spawn in December and January, (3) that retained eggs were present from December to August (no females were received in February, April, October and November), but that after January all the retained eggs, the glassy ones excepted, were undergoing absorption or disintegration, (4) that the eggs of the year, whether found with the retained eggs or not, were in the same phase of development from January to September, those of fish received July and later being a little more advanced than those of females received before July, and (5) that the ovaries of the specimens that died July 13 and September 18 were soft, but did not contain wrinkled eggs.

From these facts we conclude, (1) that the Aquarium whitefish were sexually mature in both their eighth and ninth years, (2) that in most fish spawning conditions were present in December and January and thus that the sex products of the Aquarium whitefish ripen later in the season than those of the wild whitefishes which usually spawn sometime in November and (or) early December, and (3) that the majority of the Aquarium whitefish do not spawn, but retain their eggs in the ovaries or in the body cavity where they undergo a process of absorption or disintegration. From the condition of the eggs of the year and of those undergoing disintegration in different months, it appears highly probable that the phase of rapid growth is initiated in the eggs sometime after September and completed sometime before March or February (?). The conclusion that the aquarium whitefish do not spawn agrees with the statements of Mr. Lanier to the effect that no spawning was ever observed among these fish. It may also be observed here that sexual maturity is not correlated with the size of the whitefish, but rather with its age. Thus, for instance, in Table I the eight and nine-year-old females of January 28 and May 28, which measure 219 mm. and 210 mm. respectively, are no larger than a two-year-old whitefish from Lake Huron; yet, no two-year-old whitefish has ever been known to spawn.

That sexual maturity can be a factor in the formation of annuli becomes evident when it is recalled that many species of